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SOCKER

HANDLINGAR II

COMMUNICATIONS FROM THE SWEDISH SUGAR CORPORATION

VOL. 14 • 1958 • No. 1

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1958

COMMONWEALTH MYCOLOGICAL INSTITUTE
12 DEC 195

SOCKER • HANDLINGAR II • VOL. 14 (1958) • No. 1 • PAGE 1—13

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DK 632.752.2:632 388

SUMMARY

During the period 1954—57 a large number of glasshouse tests were made to study the capacity to transmit plant virus of some 100 asexually reared strains of 6 different species of aphids *(Myzus persicae, M. ascalonicus, Aphis fabae, Aulacorthum circumflexum, Aul. solani* and *Macrosiphum euphorbiae).* The tests aimed at investigating partly the size and character of the variation in virus-transmitting ability within some of the species, especially the potato and peach aphid (*M. persicae*), partly the differences in the same respect between the species. Two virus diseases with persistent viruses were studied, namely beet virus yellows and potato leaf roll.

When certain facts had been ascertained about a number of different causes of modificatory variations in the frequency of virus transmission within one and the same strain of aphid, significant and in several cases statistically certain differences in virus-transmitting ability could be shown between different asexually raised strains of *M. persicae* concerning both yellows virus (table 3) and potato leaf roll virus (table 7). These differences between more or less effective vector strains within the same species seem to be genetically determined. In the case of certain strains such differences thus turned out to be of the same order in a number of successive tests with yellows virus over a period of more than three years. Furthermore in one of two successful cases of crosses between different strains of *M. persicae* the descendant significantly differed from the parent strains as regards the virus-transmitting ability (table 5). Another support for the view that the differences between various strains concerning infection ability are not modificatory but constitutional is that in the case of a few standard strains (nos. 3 and 10) the differences in question were of the same order regarding both yellows virus and potato leaf roll virus (tables 3 and 7).

Morphological and histological comparative tests of individual aphids from strains of *M. persicae* with differing vector effectiveness gave no information about the causes of the differences in virus-transmitting capacity.

Manifest differences in the ability to transmit yellows virus could also be observed in a small number of strains within *Aphis fabae,* where the difference between the most and the least effective strain was statistically certain (table 6). Some differences in this respect seem also to exist between different strains of *M. ascalonicus* (table 6).

Comparative tests between different species showed that an intermediary strain of *M. persicae* with regard to virus transmission was much more effective in transmitting yellows virus than strains of *A. fabae* and *M. ascalonicus.* The difference between a less effective strain of *M. persicae* and the most effective strain of *A. fabae* was quite negligible, probably even nonexistent, however. Two strains of *Macrosiphum euphorbiae,* one strain of *Aulacorthum solani* and one strain of *Aul. circumflexum* gave exclusively negative results with this virus (table 6).

Concerning the transmission of leaf roll virus *M. persicae* was also superior, since two strains (one intermediary and one less effective) turned out to be considerably better vectors than the best strain of *M. ascalonicus* and one strain of *Aul. circumflexum*. Negative results with this virus were obtained with one strain of *Aul. solani* and one strain of *Macr. euphorbiae* (table 7).

Within the investigated population of *M. persicae* the 85 strains could with regard to virus transmission be grouped in a continuous series from 10 % to 80 % average infection frequency (table 4). It has not been possible to establish any connection between the degree of the virus-transmitting capacity and the species of host plant on which the strain in question was originally found. The differences in virus-transmitting ability within the aphid species are so great that they can be assumed to influence the results of comparative tests. Therefore this variation should be taken into consideration when such work is planned.

MATERIAL AND METHODS

The extent and origin of the aphid material

The aphid material used in the tests originates from specimens collected during the years 1953—57 principally by the two authors as well as by Mr. G Möllerström. In order to increase the chances of obtaining strains of *Myzus persicae* with varying effectiveness regarding virus-transmitting capacity we have tried to represent as many different geographical and varied ecological find localities as possible in our material. Of the 85 strains of *M. persicae* included in the tests 65 came from Scania, 19 from Uppland and 1 from Västerbotten. 41 of the strains are raised from fundatrices or fundatrigeniae on peachtrees on open ground, the rest from virgogeniae. Of the latter 20 were collected on field beets, 3 on field rape, 2 on other outdoor plants, 16 in glasshouses or living apartments, 2 in mangold clamps and one in a cellar. Where several fundatrigeniae were collected on the same site they were always taken from different colonies, obviously descendants from different fundatrices. The same applies to virgogeniae collected on the same site: they were taken from plants at a long distance from one another. The origin of every strain of *M. persicae* and the other aphid species studied is stated in table 1.

Rearing of the aphid material

The aphids collected were reared in the glasshouse of the Institute of Plant Pathology and Entomology in Ultuna. The temperature in the glasshouse chambers used varied between 15° and 30° C, though as a rule it kept between 18° and 25° C. The colonies and individual specimens collected were usually first kept on a suitable host plant — for *Myzus persicae* generally a radish plant — in a pot under a glass or celluloid cylinder covered with finely meshed cotton-gauze. After a few days, when the aphids had started reproducing, one specimen was taken from each colony and placed on a suitable host in a larger cage. When a colony had formed under these new conditions the rest of the original material was discarded. As hosts for *M. persicae* radishes and broad beans were mainly used, the former in pots, the latter usually in 1/2 l. glass-bottles (in order to keep the air humidity in the cages as low as possible). At times swedes (fullgrown roots with new leaves) in Mitscherlich vessels and plants of Capsella bursa pastoris and Matricaria inodora were also used as food plants. Broad beans and beets were used as hosts for *Aphis fabae* while *Myzus ascalonicus* was reared first on shallots and later on Capsella. Capsella and Anemone coronaria served as hosts for *Aulacorthum solani* and *circumflexum*, and for *Macrosiphum euphorbiae* Capsella was mainly used. Before each test the aphid strains involved were kept for a time on the same kind of host plant and under the same environmental conditions, however.

Since it could be suspected that the host used by the aphids before infection tests might have an influence on the results, two special tests with 4 different species of host plant were made to investigate the matter. The results of these tests are recorded in table 2.

As can be seen the host plant on which the aphids were reared before the access to the virus source did not have any noticeable influence on the infection results with the same strain.

To begin with it was thought that the fundatrices and fundatrigeniae of *Myzus persicae* collected on peachtrees had to be reared on peachtree branches until a winged generation had appeared. It turned out to be impossible to keep such cut branches fresh for more than a few days. In this way some of the aphid colonies first collected were spoiled. How-

ever, it later appeared that wingless fundatrigeniae and even fundatrices from and including the last immature stage could very well be kept on radish plants. After this fact had been established the aphids collected on peachtrees were directly transferred to radish plants for culture.

As mentioned above the different aphid populations were kept in culture in bigger cages. To begin with these were of two different sizes and constructions: one larger cage of wood, cotton fabric and celluloid measuring 61×61×104 cm, and one smaller one (35×35×90 cm) of glass and wire netting with an iron-plate frame. The former cage was opened and shut by means of a zipfastener, the latter had a hinged door lined with filt. Later a number of cages of the same construction and mainly the same material as the larger type but with the dimensions of the metal cages were made. The cages with the aphids stood each on its sandfilled tray in the chamber system of the glasshouse. Each chamber accommodated 5—7 cages at the same time.

Considering the aim of the tests it was naturally of primary importance to keep the various aphid cultures well isolated from one another. The tightness of the cages was satisfactory over the whole period and their condition was kept under continual control so that possible holes could be immediately repaired or broken cages replaced by new ones. The staff attending these aphid cultures wore special protective clothing of white material while at work so that any aphids they might pick up during the opening of the cages could be easily detected and destroyed. Moreover the colonies were renewed from time to time as a matter of routine, by transferring a single specimen of each to a new host in another cage. When a new colony had thus been started the old one was destroyed. Used cages were treated with nicotine solution and cleaned before being put to use again. The periodical renewal of the populations by cultures raised from one individual aphid obviated the risk of their gradually becoming heterogeneous. Though there is no possibility of controlling this for the various strains of one and same aphid species, since they cannot be morphologically distinguished, it may be mentioned that no mixture in the same cage between two or more of the species studied *(persicae, fabae, ascalonicus, solani, circumflexum* and *euphorbiae)* was ever observed.

Method of cross fertilization

During the colder part of the year the cultures in the glasshouse were daily exposed to artificial light for some morning and evening hours thus extending "daylight time". Since the appearance of sexuales is connected with the shortening of daylight that takes place under natural conditions during late summer and autumn (de Fluiter 1950, Bonnemaison 1951, 1952, Kenten 1955), it was to be expected that the production of sexuales would be delayed or arrested. (In order to prevent this the supplementary light in the glasshouse chambers where the cages stood was temporarily shut off in October 1956). In the main this has been the case, but the various strains have behaved differently. In several strains no sexuales have ever been observed. Among the strains originating from a fundatrix or fundatrigenia taken from a peachtree this has been true of nos. 2, 4, 7, 8, 13, 15, 16, 18—23, 25—29, 43, 91, 92, 97, 99—104. Of these no. 43, collected in 1955, is still in existence while the rest have either died out or been discarded at different times. Of the strains gathered on peachtrees in 1954 no. 10 and no. 12 produced sexuales in 1954 as well as in 1955 and 1956 (in strain 10 only ♂♂ appeared in 1956, however). In strain 10, males were observed also in autumn 1957. No. 9 gave sexuales in 1954 and 1955 but died out in November 1955 probably owing to a complete transition to sexuales. Probably for the same reason no. 11 was lost in summer 1955 after having produced sexuales in autumn 1954 and in May—June 1955. The cross between 11 ♀ and 10 ♂, which produced a fundatrix in spring 1955, gave sexuales in 1955 as well as in 1956. Nos. 34, 38, 40, 41, 42, 44, 73, 90, 98, and 105 produced sexuales (♂ ♀) in the autumn of the year they were collected (1955 in some cases, 1956 in others).

Of the strains gathered on field beets nos. 14, 49, 50, 81, 109 and 110 have produced sexuales, though in the first four cases only ♂♂ were obtained. Of the strains originating in glasshouses nos. 68 and 78, both collected in 1955, produced both sexes in the autumn of the same year, while no. 70, which was also collected in 1955, only gave ♂♂. Strain 3, which descended from a virgogenia on rape in a cellar in Ultuna, produced ♂♂ already in September 1954 but has not produced any sexuales since. Strain 32, descended from a virgogenia taken from a carnation

Table 1 ORIGIN OF THE APHID MATERIAL

Myzus persicae (SULZER)

Strain no.	Descended from
1	Virgogenia on autumn rape in Sc. Bollerup 7/11 1953
2	Fundatrix on peachtree in Sc. Malmö 3/5 1954
3	Virgogenia on rape in cellar in Ultuna 5/3 1954
4	Fundatrix on peachtree in Sc. Åkarp 5/5 1954
6	Virgogenia from the culture of the Institute for Plant Protection at Bergshamra 31/7 1953
7, 8	2 fundatrigeniae on peachtrees in Sc. Övrabyborg 26/5 1954
9	„ „ a peachtree „ „ Åkarp 12/5 1954
10	Fundatrigenia on peachtree in Sc. Övrabyborg 26/5 1954
11	Fundatrix „ „ „ „ Åkarp 12/5 1954
12, 13	2 fundatrigeniae on peachtrees in Uppl. Stockholm Berg. Garden 3/6 1954
14	Virgogenia from field beets in Sc. Hilleshög 25/8 1953
15, 16	2 fundatrigeniae from peachtrees Uppl. Sthlm. Berg. Garden 3/6 1954
17	Virgogenia from Matricaria inodora in Uppl. Ultuna 30/7 1953
18—23	6 fundatrigeniae on peachtrees in Berg. Garden 3/6 1954
24	Virgogenia from field beets in Sc. Fotevik 18/10 1953
25—29	5 fundatrigeniae from peachtree in Berg. Garden 3/6 1954
31	Virgogenia on potato in glasshouse, Sc. Hammenhög 29/3 1954
32	„ „ Dianthus in livingroom, Sc. Lund 5/5 1954
33	„ „ „ „ glasshouse, Sc. Hindby 31/3 1954
34, 38	2 fundatrigeniae on peachtrees in Sc. Övrabyborg 16/5 1955
40	Fundatrigenia „ peachtree „ „ Malmö 17/5 1955
41	„ „ „ „ „ Övrabyborg 16/5 1955
42	„ „ „ „ „ Lund 23/6 1955
43	„ „ „ „ „ Arlövsgården 23/6 1955
44	Virgogenia on beets in Sc. Kävlinge 1/8 1955
46	„ „ „ „ „ Glumslöv 29/8 1955
49	„ „ „ „ „ Marieholm 29/8 1955
50	„ „ „ „ „ Hököpinge 1/8 1955
68, 69	2 virgogen. on lilies in glasshouse in Sc. Hammenhög 16/5 1955
70	Virgogenia on Stellaria media in glasshouse in Sc. St. Herrestad 16/5 1955
73	Fundatrigenia on peachtree in Sc. Malmö 18/5 1955
75	Virgogenia on Stellaria media in glasshouse in Sc. Arlöv 18/5 1955
76	„ „ Tulipa sp. „ „ „ „ V. Skrävlinge 18/5 1955
78	Virgogenia on Primula sp. in glasshouse in Sc. Arlöv 18/5 1955
81	Virgogenia on field beets in Sc. Kungstorp 23/8 1955
82	„ „ „ „ „ „ Köpingebro 26/8 1955
83	„ „ „ „ „ „ Glumslöv 21/9 1955
88	„ „ Lactuca sativa in glasshouse in Sc. on the road between Dalby and Skurup 25/10 1955
90—92	3 fundatrices on peachtrees in Sc. Övrabyborg 23/4 1956
93	Virgogenia on potted plant in Vb. Umeå Röbäcksdalen 6/4 1956
94	„ „ Hibiscus in Uppl. Uppsala 24/4 1956
95	„ „ Polygonum convolvulus in glasshouse, Sc. Hindby 24/4 1956
96	Virgogenia on Stellaria media in glasshouse, Sc. Hindby 24/4 1956
97	Fundatrix on peachtree in Sc. Lund 24/4 1956
98	Fundatrigenia on peachtree in Sc. Malmö 7/5 1956
99—105	7 fundatrigeniae on peachtrees in Sc. Malmö 14/5 1956
107	Virgogenia on field beets in Sc. Bjällerup 31/7 1956
108	„ „ „ „ „ „ Löderup 3/8 1956
109	„ „ „ „ „ „ Stridsmölla 31/7 1956
110	„ „ „ „ „ „ Tryde 3/8 1956
111	„ „ „ „ „ „ Barsebäck 7/8 1956
112	„ „ „ „ „ „ Glumslöv 27/8 1956

Strain no.	Descended from
116	Virgogenia in mangold clamp in Sc. Remmarslöv 12/3 1957
117	„ „ „ „ „ „ Glumslöv 14/3 1957
119	„ on field beets „ „ Glumslöv 7/8 1956
120	„ „ „ „ „ „ Råbelöv 8/8 1956
121	„ „ „ „ „ „ Remmarslöv 8/8 1956
201	„ „ Stachys palustris (outdoors), Sc. Glumslöv 24/10 1955
202	„ „ rape in Sc. Abbekås 24/10 1955
204	„ „ Cineraria in glasshouse in Sc. Klågerup 25/10 1955
205	„ „ field beet in Sc. Glumslöv 24/10 1955
206	„ „ „ „ „ „ „ „ „
207	„ „ rape in Sc. Vittskövle 24/10 1955
	Aphis fabae SCOP.
84	Virgogenia on field beet in Sc. Malmö 18/7 1955
85	„ „ „ „ „ „ Kävlinge 1/8 1955
86	„ „ „ „ „ „ Marieholm 1/8 1955
87	„ „ „ „ „ „ Selleberg 1/8 1955
106	Fundatrigenia on Evonymus europaea in Uppsala, May 1956
	Myzus ascalonicus DONCASTER
65	Virgogenia on Stellaria media in glasshouse in Sc. Saxtorp 15/4 1955
66	„ „ „ „ „ „ „ „ Hindby 15/4 1955
89	„ „ „ „ „ „ „ „ Dalby 25/10 1955
	Macrosiphum euphorbiae (THOMAS s. HRL.)
113, 122	2 virgogeniae from potatoes in Uppl. Uppsala, Ultuna Aug. 1956
	Aulacorthum (Neomyzus) circumflexum (BUCKT.)
115	Virgogenia from Zantedeschia in glasshouse, Uppl. Uppsala, Botanical Garden 14/11 1956
	Aulacorthum solani (KALT. s. HRL) (f. anholocyclica = Dysaulacorthum vincae Wlk. s. Börner)
114	Virgogenia on Trichosporum indoors, Uppl. Uppsala 16/10 1956

Table 2 VIRUS-TRANSMITTING ABILITY OF 4 STRAINS OF *Myzus persicae* AFTER FEEDING ON 4 DIFFERENT HOSTS

Yellows virus. Test plant: Chenopodium foliosum. 1 aphid per plant. 2 tests. 550 plants

Strain No.	*Host* Claytonia perfoliata	Beta vulgaris	Raphanus sativus	Matricaria inodora	*Mean % inf.*
3	13/40	6/20	14/40	10/30	32,7
10	25/40	23/40	26/40	12/20	61,3
12	31/40	28/40	29/40	14/20	72,5
31	14/20	29/40	26/40	27/40	68,8
Mean % inf.	60.6	57.5	59.6	57.7	

Note numerator: number of infected plants
denominator: number of colonized plants

(Dianthus) in a living room has never produced any sexuales.

Usually the sexuales occurred in October, in some cases in November and in one, no. 3 mentioned above, already in September (♂). Moreover no. 10 and 11 have each on one occasion produced sexuales in May—June.

On account of these conditions it has not been possible to cross-fertilize the different strains freely. The availability of sexuales thus limited the number of crosses that could be made. In order to prevent the pairing of ♀ and ♂ in one and the the same population ♀♀ were removed from the cages already before the last moult and placed on food plants under lamp-chimneys. This was possible since the ♀♀ of *M. persicae* can be distinguished from viviparous individuals as early as in the preimaginal instar by the colour and by the shape of the hind tibiae. When ♀ had reached the mature stage it was paired — usually in a glasstube sealed with a cotton wool plug — with a ♂ from one of the strains producing such at the same time. If no ♂♂ happened to be available, ♀ could be kept alive for a time by being put in an unheated place together with its host plant. When the sexes had been brought together pairing usually took place within a few minutes. Provided the outside temperature was not too low, ♀ was isolated upon completion of the act in a cylinder of celluloid and cottongauze tied to a branch of a peachtree standing on a trellis on the outer wall of the greenhouse or in the insectarium, which is unheated all the year round. In this way the females could lay their eggs directly on branches of living peachtrees, and the eggs could pass the winter in normal manner. In certain cases where the fertilized ♀ laid its eggs already in the pairing tube, these were glued or otherwise made to adhere to the peachtree-branches. A number of pairings took place after the temperature outside had sunk so low that the females were in danger of freezing to death on the peachtrees. They were then made to lay their eggs directly onto radishplants, but attempts to let such eggs hibernate on such plants by putting the latter in an unheated place were unsuccessful, as the eggs did not hatch in the spring.

6 pairings were made in 1954, 34 in 1955 and 40 in 1956. When the peachtrees were in bud the following springs the cylinders were inspected. All three winters the mortality amongst the eggs turned out to be very high, however. In spring 1955 only one living fundatrix, descended from a cross between strain 11 ♀ and strain 10 ♂, was found in the hibernating cages on the peachtrees. In 1956 none survived. In 1957 two individuals were hatched, both from a cross 110 ♀ × 105 ♂, but owing to an accident only one of these survived. After these fundatrices had reached the mature stage they were transferred to radish plants in cages in the glasshouse and treated in the same way as the other strains.

Virus sources, transmission methods and testplants

Introductory transmission tests with beet yellows virus with an intermediary strain of *M. persicae* concerning virus-transmitting capacity showed that infection frequency was highest when medium-aged leaves with clear symptoms from a virus-infected 1—3 months old beet were used (older and younger leaves were less effective virus sources). This is probably connected with the higher virus concentration in the medium-aged leaves, as was also shown by tests made with antiserum against beet yellows virus on sap from the different leaf categories. Continued introductory tests further showed firstly that leaves with the same symptoms but from different seed-sown beets could yield very varying transmission frequencies, secondly that older glasshouse beets (more than 4—5 months old) were weaker virus sources than younger. Such differences in the virus sources are almost certainly also due to variations in the concentration of active virus in the leaf sap and are probably connected with genotypical differences between the host plants in the first case and a decreased concentration of active virus with increasing age in the second. In order to avoid these irregularities in the virus sources leaves from 1 to 3 months old plants of a certain sugar-beet clone infected with a strain of yellows virus giving intermediary symptoms were as a rule used for the comparative tests with aphid strains. New virus-infected clone plants were successively produced by taking cuttings from older infected plants of the same clone.

The virus source used for the first comparative tests with yellows virus consisted of one picked leaf per test. This was cut into a necessary number of narrow strips parallel with the main vein, which served as virus sources to the aphid strains used in the experiment. This method was abandoned after a few tests and was replaced by feeding the

Table 3 DIFFERENCE IN VIRUS-TRANSMITTING CAPACITY BETWEEN STRAIN No. 10 AND 42 OTHER STRAINS OF *Myzus persicae* Yellows virus. Testplant: Chenopodium foliosum, 1 aphid per plant

Strain no	109	70	69	38	3	108	88	202	102	93	9	90	101	105
Number of tests	5	5	3	6	40	12	23	4	4	8	32	5	5	8
Number of plants compared	197	139	60	160	1 492	477	894	155	149	306	1 132	189	187	319
%/o of infections														
of strain 10	63.6	47.1	43.3	48.6	55.3	47.3	55.5	38.8	62.9	44.9	45.0	70.7	70.0	47.1
of strain compared	26.5	13.0	10.0	15.5	23.1	18.1	27.5	13.3	38.0	25.6	26.0	52.2	52.6	34.6
Diff. in inf. %	—37.1*	—34.1***	—33.3*	—33.1*	—32.2***	—29.2**	—28.0***	—25.5*	—24.9	—19.3	—19.0***	—18.5	—17.4	—14.5
Strain no	100	91	98	92	103	40	78	94	32	119	43	104	116	112
Number of tests	3	3	5	5	4	6	5	3	4	3	5	4	4	3
Number of plants compared	109	115	195	186	160	199	158	110	156	118	180	154	160	118
%/o of infections														
of strain 10	58.0	71.2	61.2	74.7	76.3	52.2	51.3	68.3	54.5	47.5	50.0	62.0	31.3	45.0
of strain compared	44.1	58.7	49.5	63.2	65.0	41.3	41.0	58.0	44.3	37.3	40.0	52.0	23.8	37.9
Diff. in inf. %	—13.9	—12.5	—11.7	—11.5	—11.3	—10.9	—10.3	—10.3	—10.2	—10.2	—10.0	—10.0	— 7.5	— 7.1
Strain no	41	42	14	120	107	11	76	31	12	117	110	34	111	73
Number of tests	6	3	3	4	11	10	5	8	15	4	3	5	4	10
Number of plants compared	200	89	119	159	437	389	170	312	550	160	120	127	159	338
%/o of infections														
of strain 10	54.4	45.0	38.3	61.3	43.1	45.2	48.8	45.6	54.9	31.3	60.0	45.0	46.8	53.0
of strain compared	49.1	40.8	37.4	60.8	45.2	47.4	51.1	49.4	49.0	36.3	68.5	53.7	62.5	75.6
Diff. in inf. %	— 5.3	— 4.2	— 0.9	— 0.5	+ 2.1	+ 2.2	+ 2.3	+ 3.8	+ 4.1	+ 5.0	+ 8.5	+ 8.7	+15.7	+22.6**

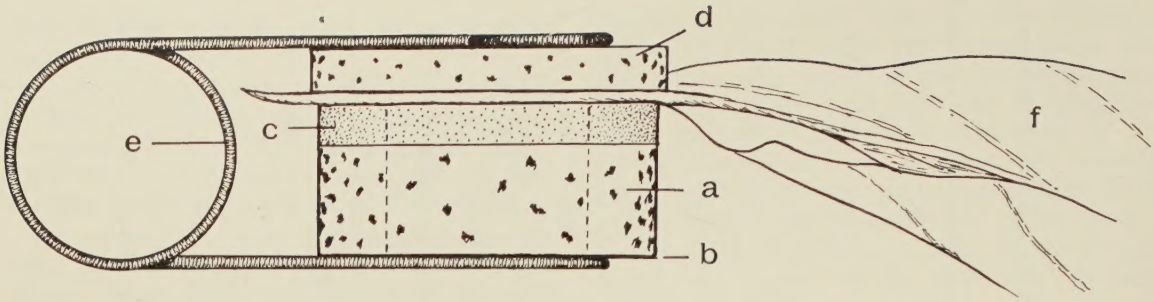

Fig. 1 Microcage for acquisition feeding on the virus source

virus-free aphid strains in microcages, which were placed directly on suitable leaves on the virus-infected clone plant.

The microcages (fig. 1) consist of an about 8 mm thick piece of cylindrical cork 25 mm in diameter (a) through which a concentric hole 15 mm in section has been drilled with a corkborer. A sheet of transparent cellophane (b) is glued over the surface turned away from the leaf when the cage is in use, while a jointing ring (c) of foamed plastic with an outer diameter of 25 mm and an inner diameter of 15 mm is fixed to the opposite side. When the cage is in use this ring presses against the nether side of the leaf (f), to which the aphids have direct access, while a loose, circular corkplate (d) 3 mm in thickness and 28 mm in section transmits the pressure of a loose metal spring (e) on the other side of the leaf, which keeps the whole thing together. Such a microcage weighs about 2.6 g.

In transmission tests with yellows virus Sylvester (1956) used microcages of a type similar to the one described above. His cages were not open towards the leaf surface, however, but provided with nylon netting through which the aphids could suck. The advantage with this type is that the insects can be directly transferred from the virus source to the test plant. On the other hand the infection frequency obtained with this method seems to be relatively low. Using one aphid per testplant Sylvester thus records successful infection in less than 10 % of the cases (1956, tables 10 and 11) while the average infection frequency in our tests was between 40 % and 50 % (table 4).

For the transmission tests with leaf roll virus infected plants of *Physalis floridana* were used. Trial tests had shown that this plant gave a higher transmission frequency than shoots or leaves from infected tubers or potato plants.

Table 4 AVERAGE INFECTION FREQUENCIES FOR 85 STRAINS OF *M. persicae*

Yellows virus. 1 aphid per testplant

Inf. frequency % ..	0—10	10—20	20—30	30—40	40—50	50—60	60—70	70—80
Number of strains ..	1	4	10	13	21	17	11	8

Table 5 VIRUS-TRANSMITTING CAPACITY OF TWO CROSSBRED DESCENDANTS OF *Myzus persicae* COMPARED WITH THE SAME ABILITY OF ONE OF THE PARENT STRAINS

Yellows virus. Testplant: Chenopodium foliosum, 1 aphid per plant. 8 and 4 tests respectively

Strain no	11×10	—	10	110×105	—	105
Number of tests	—	8	—	—	4	—
Number of plants compared	—	299	—	—	160	—
% of infections	25.5	—	59.3	32.5	—	33.8
Diff.	—	—33.8***	—	—	—1.1	—

In all cases a brush was used when moving the aphids from virus-free foodplants to virus sources and from the latter to the testplants. For yellows virus *Chenopodium foliosum* in the late cotyledon stage was exclusively used as testplant while *Physalis floridana* at the same stage served for leaf roll virus. In all tests with yellows virus only one aphid was transferred to each testplant; in the tests with leaf roll virus the number varied from 2 to 10, usually 2 aphids to each test plant. For yellows virus the aphids were kept for 24 hours on the virus source and for 24 hours on the testplant, the corresponding times for leaf roll virus being 3—5 days and 3 days respectively. During the presence of the aphids on virus sources and testplants the temperature was between 18° and 22° C. In order to kill the aphids the testplants were fumigated with nicotine and afterwards treated with a few drops of 0,05 % systox per plant. Clear and specific symptoms appeared on *Ch. foliosum* after 6 to 10 days, on *Phys. floridana* after 2—3 weeks.

Evaluation of the tests

The majority of tests included one or two strains of *M. persicae* as standards, one intermediary (no. 10) and one less effective (no. 3), which gave on an average 50—60 % and 20—30 % successful infections respectively. Great variations in infection frequency between the different tests were noted with these standards, but the difference between the virus-transmitting capacities of the two strains was constant throughout and no changes in their average transmitting capacity was observed during the three years and more they were tested. Variations in the infection frequencies in a negative direction could mainly be ascribed to two types of disturbances: insufficient concentrations of active virus in the virus sources and a weakened disposition to transmit virus during the periods sexuales appeared in the cultures. Although other types of disturbances could not be altogether avoided — as in the case of two tests that had to be discarded because the testplants had erroneously been sprayed with insecticide before use — the less satisfactory infection results in a number of experiments could mainly be traced back to one of the above mentioned causes. In reporting the results (tables 2—7) all tests where the infection frequency of the intermediary standard strain was below 20 % have been excluded. In these tests which were

Table 6 VIRUS-TRANSMITTING ABILITY OF DIFFERENT APHID SPECIES COMPARED WITH *Myzus persicae* STRAIN 10

Yellows virus. Testplant: Chenopodium foliosum, 1 aphid per plant

Species	*Aphis fabae*					*Myz. ascalonicus*		*Macr. euph.*		*Aul. sol.*	*Aul. circ.*
Strain no	85	106	86	84	87	66	65	89	122	113	114	115
Number of tests	7	5	5	6	7	7	4	5	2	3	3	4
Number of plants compared	269	159	191	209	259	237	137	197	80	120	120	160
% of infections from												
Myz. pers. strain 10	54.9	49.2	51.0	41.4	54.9	58.1	47.5	49.0	52.5	53.3	53.3	42.5
strain compared	5.1	10.0	13.7	7.3	25.4	1.7	2.6	11.3	0	0	0	0
Diff. in inf. %	—49.8***	—39.2***	—37.3*	—34.1**	—29.5**	—56.4***	—44.9*	—37.7*	—52.5**	—53.3**	—53.3**	—42.5**

Note The difference between *Aphis fabae* strains 85 and 87 is —20.3**

Table 7 VIRUS-TRANSMITTING ABILITY OF DIFFERENT APHID SPECIES

Leaf roll virus. Testplant: Physalis floridana, 2 aphids per plant. 4 tests

Species	*Myzus persicae*		*Myz. asc.*	*Macr. euph.*	*Aul. sol.*	*Aul. circ.*
Strain no	3	10	89	113	114	115
Number of testplants	80	80	80	80	80	80
% of infections	46.3	71.3	17.5	0	0	17.5
Diff. in inf. %						
from strain 3	—	+25.0**	—28.8***	—46.3***	—46.3***	—28.8***
from strain 10	—25.0**	—	—53.8***	—71.3***	—71.3***	—53.8***

considered abnormal and of little value for comparison, no infections were generally obtained with the less effective standard strain.

Altogether 157 comparative tests with 60—120 testplants in each were made with yellows virus. Of these 23 were discarded for the reasons mentioned above. 12 tests with 20—120 testplants in each were made with leaf roll virus. One of these was rejected. Usually 20 testplants per test were made for each aphid strain. In a number of cases one or a couple of testplants died of root-rot or other causes before the symptoms appeared. When this occurred the infection frequencies were counted on the number of surviving plants, which accounts for the fact that the number of plants compared in tables 3—6 is quite often irregular.

STUDIES CONCERNING THE VARIATIONS IN VIRUS-TRANSMITTING ABILITY WITHIN MYZUS PERSICAE

Earlier investigations

Earlier studies of *Myzus persicae* in this respect have been relatively few. On the basis of 4 experiments Stubbs (1955) reports significant differences between "clones" of *persicae* in their capacity to transmit an undescribed virus on spinach. The "clones" compared seem to originate from one and the same aphid colony on a healthy spinach-plant. In spite of this one may conclude from the results of the tests that this population was heterogeneous.

Day (1955) compared 20 "clones" of *Myzus persicae* in their capacity to transmit the leaf roll virus of potatoes. These "clones" originated from selected individuals of one and the same population, the descendants of a number of winged aphids collected in the field. Thus the original population was in all probability heterogeneous. From this material mature apterae had been selected for an infection test, and of these 20 were permitted to reproduce in separate cultures, which were later compared in new tests. The result was negative, since no constant differences could be observed, but Day believes that more extensive tests are necessary before any conclusions can properly be drawn. It should be noted that the way in which the mothers of the "clones" tested by Day were selected does not seem to have guaranteed the preservation of the original heterogeneity in the test material.

Own investigations

Tests with yellows virus

Testing the aphid strains collected. All in all 85 collected strains of *M. persicae* were tested. Regarding the extent of the tests the material may be suitable divided into two groups:

Group 1 43 strains compared in 3 or more tests with some standard (table 3).

Group 2 42 strains compared in 1 or 2 tests with some standard.

The material in group 1 is recorded in table 3, compared to standard strain 10 and grouped according to the extent of the differences. A fairly even series from the minus difference 37.1 to the plus difference 27.6 was obtained. In this series the standard (no. 10) is somewhat deflected to the plus-side, with 32 strains with a lower and only 10 strains with a higher infection frequency. 8 of the minus differences and 1 of the plus differences are significantly separated from the standard. Since marked variations in the average infection frequency were noted between different tests, it is probable that an

increase in the number of tests would in certain comparisons have enhanced the number of significant differences both on the plus- and the minus-side.

It should be noted that some of the less effective strains in table 3 are purposely so selected as to be overrepresented, for which reason the table does not reflect the true distribution of vector strains with different effectiveness within a large natural population of *M. persicae*. A better picture of this distribution is presented in table 4, in which all the investigated strains of this species are recorded.

Further comparisons between certain strains within group 1 were made possible by tests without standard strain 10 and thus not recorded in table 3. A varying number of tests was made to compare some of the less effective strains, namely nos. 3, 9, 38, 88 and 108, while some more effective strains, nos. 12, 31 and 34 were compared in another set of experiments. The absolute infection frequencies for the different strains were of the same order as in table 3, but none of the differences from 2—10 % in the two comparative series were significant.

Within group 2 the 42 strains were tested together with some standard either on one occasion (12 strains) or on two (30 strains). The primary aim of these less comprehensive comparisons was to find extreme variants regarding the virus-transmitting capacity to be used in further studies. First and foremost wholly ineffective strains were sought for purposes of crossing and morphological studies. Though no such strains were actually found, there were a number of less effective ones. These were tested in succeeding experiments and transferred to group 1, where they thus came to be overrepresented. The 42 remaining strains in group 2 had infection frequencies fairly evenly grouped around the relatively effective standard strain 10. At the stage the investigation had reached at that time no great importance was attached to these strains. It may, however, be possible that some of most effective among them (especially those 7 whose infection frequencies were preliminarily determined at 70—80 %) might in continued tests have turned out to be much more effective than standard strain 10 (cf. strain 73 in table 3).

A combination of groups 1 and 2 (table 4) shows the distribution of infection frequencies for all the strains of *M. persicae* investigated.

The even distribution of infection frequencies within the population investigated does not indicate the presence of certain well-defined groups of more or less effective vector strains, but rather that the species contains a continuous series of strains with different infection capacities. Moreover an examination of the origin of the different strains does not show any connection between the original species of host plant and the infection capacity regarding yellows virus. Thus table 4 contains representatives from peachtrees, beets and other plants on the whole evenly divided into less effective, intermediary and more effective vector strains.

The absolute differences in infection capacity are considerable between some of the strains and significant in several cases (table 3). Considering the method used (only one aphid per testplant) the majority of the investigated strains can be said to be very effective vectors. In other transmission tests with yellows virus and with three or more aphids per testplant an infection frequency of 100 % has often been achieved by intermediary and more effective strains. The differences in infection capacity within the species are so great, however, that they can evidently influence the results of comparative virus transmission tests. When planning such experiments this variation should therefore be taken into consideration, and preliminary tests should be made to avoid the use of especially negative extreme variants.

Tests with strains obtained by cross breeding. Although 80 cross combinations between 18 different strains of *M. persicae* were made, only 2 of these gave issue. The two new fundatrices were asexually reared to produce new strains and these were compared with one of the parent strains regarding their virus-transmitting capacity. During the long period required for the maturing and hatching of the eggs and for the asexual rearing of the descendants one of the parent strains (no. 11) was unfortunately lost in one of the cases (11×10), probably owing to total transition to sexuales; in the other case (110×105) one of the parent strains (no. 110) was accidentally destroyed.

Table 5 shows that the descendant of crossbreeding 11×10 was to a high degree and markedly different from strain 10. The 8 comparative tests were carried out at different times of the year between the 1st July 1955 and the 7th August 1956. Since 10 comparative tests had previously shown the pa-

rent strains 10 and 11 to be practically alike regarding virus transmission (table 3), it may be concluded that the crossbred descendant in this case had a considerably lower virus-transmitting capacity than both parent strains. The descendant of cross 110×105, where previous tests had shown the parent strains to be quite different regarding virus-transmitting capacity (table 3), did not differ from strain 110 in this respect, as shown by comparisons recorded in table 5.

The result obtained with cross 11×10 lends good support to the view that the differences between various aphid strains regarding virus-transmitting ability are genetically determined.

Tests with leaf roll virus

Aphid strains 3 and 10 were compared in 7 acceptable tests with altogether 270 testplants of *Physalis floridana*. The average infection frequencies were 50.8 % and 79.3 % respectively. The difference of 28.5 % is statistically sure on the 5 % level (*) and certainly somewhat smaller than the corresponding difference with yellows virus (32.2***, table 3), though of the same order of magnitude. In the 4 comparative species tests with the same virus (table 7) the difference was statistically more certain (25.0**) and about as great as in the 7 tests mentioned above.

The similarities in type and extent of the differences in virus-transmitting ability regarding two different viruses lends additional support to the assumption that these differences between two aphid strains are not modificatory but constitutionally determined.

Morphological and histological studies

Our original plan included the carrying out of morphological comparisons between strains of *Myzus persicae* different with regard to virus-transmitting capacity. These comparisons aimed partly at establishing possible outward differences by which the various strains could be identified, partly at studying anatomical differences that might contribute to an explanation of the causes for the differences in vector efficiency found. In this way our understanding of the mechanism governing the transmission of persistent virus in general could be improved.

Concerning the first of these aspects measurements of the length of the antennal segments in different strains were begun in 1954. Earlier investigations by Waldhauer (1953) had seemed to show that the anholocyclic form of *M. persicae* ("*Myzodes dianthi* SCHRNK." sensu Börner) was on the average different from aphids of fundatrigenous origin concerning the relation between the length of the base of the last antennal joint and the processus terminalis. Differences in the colour of the body had also been reported. Since subsequent investigations by F P Müller (1954) show that such differences apparently disappear in older cultures, it seemed of little value to pursue the matter and the study in question was dropped.

The investigations concerning possible anatomical differences have so far been confined to an introductory study on microtome sections of the structure of the mouth parts and the intestinal wall of *Myzus persicae*. The limitations of the technical resources at present at our disposal have, however, made it difficult for us to proceed beyond the facts already established by Weber (1928) whose exemplary examination of the structure of the mouth parts and intestine of *Aphis fabae* had the same purpose as ours — to clarify the mechanism governing virus transmission. We have therefore decided to postpone further anatomical studies until we have access to an ultramicrotome for electron microscopy.

STUDIES CONCERNING THE VARIATION IN VIRUS-TRANSMITTING ABILITY BETWEEN APHID SPECIES

Earlier investigations

Earlier studies dealing with the part played by various aphid species as vectors of different viruses have as a rule confined themselves to establishing whether the species concerned actually possessed the ability to transmit virus. Quantitative comparisons are relatively few. Some examples may be quoted. Thus Kassanis (1942) compared "*Aphis rhamni*" (probably = *Aphis nasturtii* KALT. sensu Börner) with *Myzus persicae* as vector for virus Y of the potato, and reached the conclusion that both are equally effective. In 1938 Dykstra and Whitaker compared the species *Myzus persicae*, "*Myzus*" *solani* and *Macrosiphum solanifolii* as vectors of potato leaf roll virus amongst others. Their statistical results are, however, based on tests in which testplants and virus sources infested by aphid populations stood in the same cages.

The number of active aphids is thus unknown. According to Watson (1946) *Aphis fabae* is less effective in transmitting beet yellows virus and beet mosaic virus than *Myzus persicae*. Doncaster and Kassanis (1946) compared *Myzus ascalonicus* DONCASTER with *Myzus persicae* as transmitters of 8 viruses, among them beet yellows virus. In these tests the number of aphids per testplant differed for the two species. MacCarthy (1954) reports the results of his transmission tests with potato leaf roll virus and the vectors *"Myzus" solani* KALT., *Myzus ornatus* LAING, *Macrosiphum solanifolii* ASHM., (= *euphorbiae* THOMAS), *Aphis gossypii* GLOVER and *Myzus persicae* (SULZER).

Own investigations

Tests with yellows virus

Altogether 12 strains of 5 different aphid species were compared with strain 10 of *Myzus persicae* in a varying number of tests (table 6). In other tests some of the strains were also compared with strain 3 of *M. persicae*.

The five strains of *Aphis fabae* were throughout considerably less effective than strain 10. There were great differences in absolute infection frequency between the various strains of *A. fabae*, and the difference between the least and the most effective (no. 85 and no. 87), which were compared in 7 tests, was statistically certain. In a comparison consisting of 6 tests with 228 testplants strain 87 of *A. fabae* was practically the same as the less effective strain 3 of *M. persicae* concerning average infection frequency (26.9 % and 28.8 % respectively), thus indicating that the populations of these aphid species are not entirely unlike regarding infection ability on individual plants. The fact that in nature *M. persicae* is undoubtedly the more important vector must be connected with its considerably greater mobility, which enables it to create secondary infections in plants around a primarily infected one (Björling, 1952).

The average infection frequency for *M. ascalonicus* was even lower than the corresponding frequency for *A. fabae*. Differences in virus-transmitting capacity also seem to exist between the 3 strains of *M. ascalonicus*, but it has not been possible to establish from the present tests to what extent the differences between the most effective (no. 89) and the other two are real, since only one comparative experiment was made with all three strains together.

Entirely negative results were obtained with the examined strains of *Macrosiphum euphorbiae*, *Aulacorthum solani* and *Aul. circumflexum*.

Tests with leaf roll virus

Four aphid species suspected of being vectors of leaf roll virus were represented by 1 strain each in 4 comparative tests with strains 3 and 10 of *M. persicae*.

Apart from the two strains of *M. persicae* whose mutual relationship was about the same as in the tests with yellows virus (table 3), positive results were also obtained with *M. ascalonicus* and *Aulacorthum circumflexum*. The average infection frequencies of the two last named species were similar and considerably weaker than the corresponding values for the two strains of *M. persicae*. The tested strains of *Aul. solani* and *Macrosiphum* gave negative results.

This investigation has been financially supported by the Agricultural Research Council and the Swedish Sugar Co. L Grytell, G Ljungberg, K Rydén and L Wilkens assisted in the experimental work.

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Skånska Litogr. AB., Malmö 1958

Publisher:

Svenska Sockerfabriks Aktiebolaget

Postbox 258 Malmö

Distribution:

C W K Gleerups Bokförlag, Lund

postgironr 30843

Responsible Editor: **S O Månsson**

The price of this part:

2,00

Swedish crowns

Skånska Litogr. AB., Malmö 1958